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# Light-growth responses of Sitka spruce, Douglas fir and western hemlock regeneration under continuous cover forestry

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## Abstract

Natural regeneration is crucial for silvicultural approaches based on the continuous presence of a forest cover, or Continuous Cover Forestry (CCF). Light is considered one of the most important factors affecting regeneration growth under canopy cover. Sitka spruce, western hemlock and Douglas fir are important forestry species both in Europe and in North America with potential to be used together under CCF management. Our aim was to develop predictive early-growth models for these species growing beneath forest canopies, and to investigate species differences in terms of shade tolerance.

We sampled regenerating trees growing under canopy cover at multiple sites in the UK. We compared alternative asymptotic non-linear models as a function of light availability to

simulate the height growth for all species and the diameter growth for Sitka spruce and western hemlock only. We included tree size and intra-regeneration competition as predictors, which affected the asymptotic growth at full light and/or the growth rate at which such asymptote was reached. We also calibrated models of apical dominance ratio (ADR, for all species) and live crown ratio (LCR, for Douglas fir and Sitka spruce only) as a function of light availability, tree size and intra-regeneration competition.

Species-specific non-linear models best simulated the light-growth responses (3-points Logistic for Sitka spruce, Michaelis-Menten for western hemlock, asymptotic with offset for Douglas fir). Tree size in all cases increased the asymptotic growth and in two cases also the growth rate. Competition significantly reduced the growth for Sitka spruce and western hemlock, with the diameter growth reduced more than height growth. Both the ADR and the LCR increased with light availability, with species-specific differences for LCR but not for ADR. For Sitka spruce an apical dominance ratio of 1.5 can be used in the field to identify adequate growing conditions. An increasing shade tolerance ranking was found as Douglas fir  $\leq$  Sitka spruce < western hemlock.

We conclude that modelling light-growth requires species-specific non-linear functions and that predictions are improved by including size and competition. The developed predictive models for height and diameter growth will allow accurate modelling of the study species in CCF management.

## **1.1 Introduction**

Continuous cover forestry (CCF) is a range of silvicultural approaches involving uninterrupted maintenance of forest cover and avoidance of clearcutting (Pommerening and Murphy, 2004), is becoming increasingly important worldwide (Schütz et al., 2011). Mason et al. (1999) indicated the following principles for CCF: management of the forest ecosystem rather than

just the trees; use of natural processes as the basis for stand management; adaptation to site limitations; and creation of a diverse stand structure with a range of species. Amongst the consequences of those principles, there is an increasing focus on the use of natural regeneration to develop uneven-aged and mixed-species stands (Pommerening and Murphy, 2004).

Light is considered one of the main factors affecting tree regeneration under forest cover (Lieffers et al., 1999; Oliver and Larson, 1996). Measurements of the light regime under canopy have been widely used as main inputs for regeneration growth models, especially in uneven-aged and mixed-species stands (Duchesneau et al., 2001; Finzi and Canham, 2000; Grassi and Giannini, 2005; Ligot et al., 2013; Pacala et al., 1996; Wright et al., 1998). Canopy characteristics, and in turn light analysis based on those characteristics, are better predictors for regeneration growth models than traditional stand parameters, such as stem density or tree volumes, especially in uneven stands (Chrimes and Nilson, 2005; Peng, 2000).

We focus here on three important forestry species in Europe and North America with potential to be used together in CCF systems. Sitka spruce (*Picea sitchensis* (Bong.) Carr.) is an important forest species in its original range, the Pacific North-West of America, and it is the most common introduced non-native tree species in Atlantic Europe, covering about 1.3 million hectares (Mason et al., 2011; Nygaard and Øyen, 2017). In the United Kingdom (UK) it is the main commercial tree species, comprising alone about a quarter of the total forest cover (Forestry Commission, 2017). Sitka spruce reproduces abundantly across all the UK (Nixon and Worrell, 1999) and its potential for CCF management has already been positively tested in many experiments (Mason, 2015). Western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco), both associates of Sitka spruce in its natural range, are other successfully introduced coniferous species in the UK that could be adequate companions of Sitka spruce in mixed-species, uneven-aged forests (Cameron, 2015). Mixed regeneration of these species is already found occurring naturally in the UK. However,

there are no general predictive models of the early growth of these species growing under the range of light regimes encountered in CCF systems.

Interspecific differences in shade tolerance significantly affect stand dynamics (Finzi and Canham, 2000). For Sitka spruce, Mason (2015) indicated that in the United Kingdom regeneration under canopy cover requires at least 20-25% of full light for a growth about half that under full sunlight. Carter & Klinka (1992) in British Columbia (Canada) found that for Douglas fir that happened at 20-40% of full light, and for western hemlock at 10-20% of full light. Generally, western hemlock was considered the most shade-tolerant of the three species by all authors, while Sitka spruce was found to be either more than, less than or equally shade-tolerant to Douglas fir (Malcolm et al., 2001; Mason et al., 2004; Minore, 1979). Shade tolerance, the ability to grow and survive under low levels of light, is an elusive property; ecologists have not yet agreed on a standardized method for its quantification (Lusk and Jorgensen, 2013), and many characteristics have been used to define a shade tolerance ranking amongst species. Shade-tolerant species usually show relatively faster growth at low light and a slower growth at high light than less shade-tolerant species, although this trade-off is not necessarily clear-cut (e.g. Pacala et al. 1996). Usually, shade-tolerant species show a complementary trade-off between higher capacity for surviving at low light with lesser growth at high light (Kobe and Coates, 1997). Other authors define as more shade-tolerant the species that reach the whole-plant compensation point at lower light levels (Lusk and Jorgensen, 2013). Crown plasticity is another characteristic usually associated with shade tolerance. Shade-tolerant trees growing under low light levels can modify their crown architecture to a more efficient shape for light absorption, by expanding it more horizontally than vertically, and by limiting the number of living lower branches, which are generally more shaded (Claveau et al., 2002; Lieffers et al., 1999; Williams et al., 1999). In shade-tolerant trees this would result in a reduction in the apical dominance ratio (ADR), the ratio between the length of the leader and

of the lateral shoots of the same year, and also a reduction in the live crown ratio (LCR), the ratio between the height of the live crown and the tree height. In other words, shade-tolerant trees tend to form an “umbrella-shaped” crown under low levels of light (e.g. O’Connell & Kelty 1994), which allow them to survive long periods of shading from the overstorey. ADR can be also used in the field as a quick tool for identifying whether a tree is growing under sufficient light conditions (e.g. Page et al., 2001).

There is a growing consensus that theoretically-justified non-linear models are best suited to describe plant growth (Paine et al., 2012). Such models are based on specific hypotheses regarding the phenomenon to be described and use parameters that have a clear biological meaning (Fekedulegn et al., 1999). In the case of the light-growth response of regenerating trees, asymptotic non-linear functions have been commonly used, such as the Michaelis-Menten and the Logistic (Ligot et al., 2013; Pacala et al., 1996; Paine et al., 2012): with increasing values of input (light), the response (growth) increases but eventually saturates and reaches a maximum value at a certain level of input. The two functions differ in the way the growth rate reaches the asymptote. The Michaelis-Menten always has a concave-down shape that passes through the origin (growth is zero at no light). The Logistic, in its “three-points” form, has a sigmoid shape that confers better flexibility, but while it has a lower asymptote set to zero, it is not constrained to pass through the origin (growth can be positive at zero light). Ecological theory suggests that trees under low light levels could reach a “compensation point” at which the photosynthesis equals the respiration costs, thus showing no growth at positive light levels (Givnish, 1988). The asymptotic function with an offset (Pinheiro et al., 2016), from here on called Asymptotic-with-offset, can resolve this issue: it is an always concave-down function (in this regard similar to the Michaelis-Menten) but is not constrained to pass through the origin. The growth can be equal to zero at a positive value of light, and the intersect

of the curve with the x-axis would be the compensation point as defined above. See Figure 1 for examples of the three different equations.

Most previous non-linear light-growth studies have assumed the same response curve for trees of different size by using the relative growth rate, that is by scaling the absolute growth by the tree size (e.g. (Pacala et al., 1996). However, relative growth rate usually decreases with increasing tree size due to biological and geometrical issues (Paine et al., 2012). Photosynthetic efficiency is also expected to change with tree height: taller trees can have an advantage in better exploiting light resources, but that ability comes with higher respiration maintenance costs (Givnish, 1988; King, 1990). Claveau et al. (2002) reported that the way in which tree size affects light-growth responses has not been widely studied, and they suggested incorporating it as a predictor in future studies.

The presence of intra-regeneration competition could be another factor significantly affecting the light-growth response. Intra-regeneration competition was found to significantly affect growth either only at higher light levels (Duchesneau et al., 2001); only the radial but not the height growth (Collet and Chenost, 2006; van Couwenberghe et al., 2013); only if the trees were overtopped (Hasenauer and Kindermann, 2002; Ligot et al., 2013); or not at all (Grassi and Giannini, 2005; Monserud and Ek, 1977). As far as we are aware only Ligot et al. (2013) used specific non-linear models where tree size and intra-regeneration competition were included as additional variables modifying the asymptote of the functions, albeit not the growth rate to reach it.

The general aims of this study were to expand the knowledge of the light-growth response of Sitka spruce, western hemlock and Douglas fir in the understorey and to inform modelling for forestry operators interested in CCF. To do so, we investigated regenerating trees growing under canopy cover to evaluate:

- 1) The species-specific light-growth responses (in both height and diameter), under the range of light regimes encountered in CCF systems, comparing different non-linear models that include also tree size and intra-regeneration competition;
- 2) The species-specific crown plasticity (in terms of apical dominance ratio and live crown ratio) under different light levels, how this process is affected by tree size and intra-regeneration competition, and whether the apical dominance ratio can be an indicator of the growth condition of the tree;
- 3) If the resulting light-growth and crown plasticity responses can be used to identify a shade tolerance ranking.

## **1.2 Methodology**

### **1.2.1 Data collection**

The study areas included a wide range of forests across the UK, divided into various stands dominated by different overstorey species (see Table 1 for more details). For each stand, we laid out ten plots with a random-systematic approach. We drew random non-parallel transects on a desktop map and placed on them evenly-spaced plots, later located in the field using a GPS receiver. The distance between plots varied with the size of the stand. For each plot, we selected the closest Sitka spruce (SS), western hemlock (WH) and/or Douglas fir (DF) naturally regenerating tree, excluding trees with evident sign of browsing or other kinds of damage. Trees were classified into broad height classes, and for subsequent plots we chose trees belonging to a different class to ensure a balanced sample range. Recent silvicultural management in each stand varied from no intervention to thinning of different intensity and type, but purposely we selected no stand thinned in the last two years. We also relocated plots that fell in areas with recent windblow events if possible; otherwise, we discarded them. While all SS and WH seedlings were natural regeneration, one-third of the DF seedlings measured



168 were artificially under-planted (all those in Clocaenog and some of those in Wykeham). Data  
169 collection was carried out from February to November 2016.

170 On each tree, we measured the height growth (Hg) as the length of the last complete leader  
171 shoot, and the tree height previous to that growth (Hp) as the total height minus the height  
172 growth. We calculated the apical dominance ratio for SS and DF (not for WH due to its different  
173 canopy architecture) as the ratio between the corresponding leader and lateral shoots for both  
174 the last complete vegetative season and the previous one (called respectively ADR and ADRp).  
175 Note that we measured the largest and shortest one lateral shoot per tree and reached an  
176 average. We calculated the live crown ratio (LCR) as the ratio between the length of the stem  
177 from the top to the lowest live green branch and the total height. In all cases we discarded from  
178 the measurements any incomplete shoots found if the survey was carried out during  
179 spring/summer. The tree measurement schematics are displayed in the Supplementary  
180 Information. For SS and WH trees, we collected a stem sample at 10 cm above the root collar,  
181 unless the tree presented an evident swelling, a common occurrence for large regenerating  
182 trees, in which case no sample was collected. For DF, we could not collect any stem samples  
183 due to particular forest management prescriptions. For each stem sample, we measured with an  
184 optical microscope the diameter growth (DRCg) as twice the width of the last tree ring, and the  
185 diameter previous to that growth (DRCp), as the total diameter under bark minus the diameter  
186 growth. We took all the measurements in two directions (the shortest and longest diameter for  
187 each sample) and averaged the values. As above, we discarded from the measurements any  
188 incomplete rings if the survey was carried out in spring/summer.

189 We assessed the intra-regeneration competition by counting the number of regenerating trees  
190 of all species around the subject tree. If the subject tree was under 130 cm height, to count the  
191 competition we used a circle of 80 cm radius from its stem (around 2 m<sup>2</sup>), if 130-250 cm height,  
192 a circle of 120 cm radius (around 4.5 m<sup>2</sup>), and if above 250 cm height a circle of 160 cm (around

8 m<sup>2</sup>). We then added one and log-transformed the number, to create the variable *comp*, indication of the competition at plot level, not transformed per area unit. While circular 2 m<sup>2</sup> plots have been previously used for trees 20-180 cm tall (van Couwenberghe et al., 2013), we decided to compensate for the increasing crown radius of bigger trees by using larger circles based on empirical observations on the ground (i.e. a circle of radius 80 cm centred on a stem of a 5 m tall tree in most cases did not extend beyond its crown).

#### 1.2.1.1 Hemispherical photography

At the top of each tree, we took hemispherical photography (HP) images using a Nikon Coolpix (4500 or 990 model), equipped with Nikon FC-E8 183° FOV Fish-Eye Converter Lens. We carried out the circular HP image acquisition on windless days, under overcast sky conditions or after sunset (Fournier et al., 1996). In stands with the presence of broadleaved trees, we acquired the images during summer to have the full foliar development of the overstorey. We positioned the camera on a telescopic pole, oriented to the North using a compass and upwards to the zenith using a level. We took a picture using the automatic exposure and then more in quick succession with reduced exposure bias to obtain at least one picture with good contrast (Hale et al. 2009). For image processing, we used the protocol of Bianchi et al. (2017). We automatically thresholded the pictures using the function *enhanceHemiphoto* of the package *Caiman* (Diaz and Lencinas, 2015) from the R Statistical Software (R Core Team, 2017). Using CIMES-FISHEYE (Gonsamo et al., 2011), we estimated: canopy openness (CO), the unobstructed fraction of the sky hemisphere viewed from a single point (Gonsamo et al., 2011); indirect site factor (ISF) and direct site factor (DSF), respectively the transmittance through the canopy of the diffuse light from an overcast sky (considering a Standard Overcast Sky model) and of the direct light from a clear sky (Hale et al., 2009). We calculated the global site factor (GSF), the total radiation that comprises both those components, as shown in Equation 1 (Met Office, 2006).

$$\text{Equation 1 : } GSF = 0.65 * ISF + 0.35 * DSF$$

## 1.2.2 Statistical analysis

We carried out all the analyses with the package *nlme* (Pinheiro et al., 2016) of the R Statistical Software (R Core Team, 2017).

### 1.2.2.1 Height and diameter growth models

We modelled *growth*, either Hg (for each species) or DRCg (for SS and WH), as a function of *light*, the GSF estimated from HP, comparing three asymptotic non-linear functions based on the Michaelis-Menten (Equation 2), the 3-points Logistic (Equation 3), and the Asymptotic-with-offset (Equation 4). Our rationale was to observe which function best fitted the growth process in each case and then derive the corresponding biological implications.

$$\text{Equation 2: } Growth = \frac{r + Asym * light}{xmid + light}$$

$$\text{Equation 3: } Growth = \frac{r + Asym}{1 + \exp^{(xmid - light)/scale}}$$

$$\text{Equation 4: } Growth = (r + Asym) * (1 - \exp^{-\exp(lcr) * (light - cp)})$$

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Where:

$$Asym = (A + A2 * comp) * size^{Pa}$$

$$xmid = (K - K2 * comp) / size^{Pk}$$

$$lcr = (K + K2 * comp) * size^{Pk}$$

$$scale = S / size^{Ps}$$

$$cp = C / size^{Pc}$$

In all equations, *Asym* indicates the asymptotic maximum growth that is reached at high light levels, and *xmid* and *lcr* how fast the growth reaches this asymptote (i.e. the growth rate). In

Equation 2 and 3, *xmid* represents directly the value of light about which the growth is half of the asymptotic growth, or simply half-maximum-growth. In Equation 4, *lcr* represents the same, but after a transformation (see Supplementary Information). Then, *scale* in Equation 3 represents the steepness of the curve around the sigmoid inflection point, and *cp* in Equation 4 the compensation point, the level of light corresponding to zero growth. We included *size*, either the height or diameter before the growth (*Hp* or *DRCp*), in each of those terms, with an effect mediated by the coefficients *Pa*, *Pk*, *Ps* and *Pc*. We included competition (*comp*) only in the terms related to the asymptotic growth and the growth rate, with an effect mediated by *A2* and *K2*. We did not include a competition effect for *scale* in Equation 3 since it would not have had any biological validity, or for *cp* in Equation 4 for computational simplicity. We included *r*, a random factor at forest level affecting the value of asymptotic growth, to take into consideration the possible auto-correlation of the plots in the same forest due to the site fertility or local climatic conditions. It must be noted that the growth rate increases with lower values of *xmid*, and the opposite for *lcr*. In other words, the asymptote is reached faster in Equations 2 and 3 for lower values of *xmid*, and in Equation 4 for higher values of *lcr*. The sign on the *K2* parameter and the inclusion of *size* (as multiplicator or dividend) were adjusted to ensure a consistent direction of response for the *xmid* and *lcr* variables. The summary of the biological implications of each coefficient is shown in the Supplementary Information. We also tested equations in which *size* had opposite effects on *xmid/lcr*, *scale*, and *cp* than indicated on the previous equations but the models did not fit.

For each combination of growth and species, we tested the three base functions, and all their possible combinations where some or all the main coefficients (*A*, *K*, *S* and/or *C*) were not affected by size (setting *Pa*, *Pk*, *Ps* and/or *Pc* to 0) or by competition (setting either *A2* and/or *K2* to 0). Preliminary results showed that when the competition was affecting both asymptotic growth and growth rate (by setting both *A2* and *K2* to non-zero values), it led to unrealistic

biological responses, so we discarded such models. There were 12 models belonging to the family originated from the Michaelis-Menten function, and 24 each for the Logistic and Asymptotic-with-offset, a total of 60. To consider the heteroscedasticity of the data, we modelled the variance as a power of the fitted values, with the power determined during model fitting. For each combination of species and type of growth, we pooled together all the models belonging to the different families. We selected as candidates the model with the lowest Akaike Information Criterion (AIC) and those within two AIC units. Then, in each case we chose the best model as the one with the highest parsimony (fewest parameters affected by size and competition), and in the case of a tie, with the best prediction performance (lowest AIC) and better biological validity (by observing the simulated growth pattern). For each best model, we calculated the Pearson's correlation coefficient  $r$  between simulations and observations, and the simulation errors in terms of Root-Mean-Square-Error (RMSE), Mean Absolute Error (MAE), and Mean Absolute Percentage Error (MAPE), that is the MAE relative to the observed growth (Hyndman and Koehler, 2006).

To compare growth patterns across species, we also calculated the light level necessary to obtain the half-maximum-growth for all best models. In case of the Michaelis-Menten and the Logistic, that was directly equal to  $x_{mid}$  (calculated using the coefficient  $K$  and the influence of  $K_2$  and/or  $P_k$ ), while for the Asymptotic-with-offset, it was estimated starting from  $lcr$  (again accounting for the influence of  $K_2$  and/or  $P_k$ ).

#### 1.2.2.2 Apical dominance ratio (ADR) and live crown ratio (LCR) analyses

Using a dataset where all species were combined, we calibrated Generalized Linear Mixed Models (GLMMs) for ADR (only for SS and DF) and LCR. In both cases we used as predictor variables: species, light (GSF), size (Hp) and competition (*comp*), including two-way interaction terms between all variables. We included a random intercept effect at forest level to account for spatial autocorrelation. After observations of the data distribution and

preliminary modelling results, we decided to use log-transformed GSF and Hp for a better fit. From the global model with all variables, we then tested structures with fewer fixed effects, and selected as the best model the one with lowest AIC. In the cases where models had differences of less than 2 points, we chose the model with fewer explanatory variables. We modelled the height growth (Hg) as a function of the previous year's apical dominance ratio (ADRp) and tree height (Hp). After preliminary modelling, for both species we observed better results in terms of AIC using a Logistic non-linear equation, as shown in Equation 5, than a GLMM.

$$\text{Equation 5: } Hg = \frac{r + A * Hp^{Pa}}{1 + e^{(K - ADRp)/S}}$$

## 1.3 Results

### 1.3.1 Growth models

For SS, we selected as best a model from the Logistic family for both height and diameter growth; for WH, from the Michaelis-Menten again for both height and diameter growth; and for DF/Height, from the Asymptotic-with-Offset. Table 2 presents the coefficient values of those models, showing the main model components (asymptotic growth, growth rate, scale and/or compensation point) affected either by the tree size (if Pa, Pk, Ps and/or Pc ≠ 0) or by the intra-regeneration competition (if A2 or K2 ≠ 0). The estimated growth patterns for each model versus the observations are shown in Figure 2. See Supplementary Information for the AIC values of all the models fitted, and the confidence intervals of the predictions. In all cases but for the WH/Height model, tree size affected the asymptotic growth (Pa > 0) and consequently, the absolute growth was higher for bigger trees at all light levels. Absolute growth was higher for taller trees also for the WH/Height model within the data range observed, even if Pa = 0, due to the effect of Pk > 0. However, the analysis for western hemlock could have been biased due to the lack of sampled trees growing at high light levels and of an

asymptote reached outside the data range. For SS/Height and WH/Height, tree size affected the growth rate ( $P_k > 0$ ): bigger trees had a higher growth rate than smaller trees, more markedly at lower light levels. Only for DF/Height, tree of all sizes showed in the simulations a compensation point above zero light (around GSF 0.08, the value of the coefficient C), due to the Asymptotic-with-offset being chosen as base for the best model. Since both the WH models were based on Michaelis-Menten, the compensation point was set at zero light for that species. Sitka spruce, since Logistic was selected for both the height and diameter best models, had an estimated positive growth at zero light. While the positive growth at zero light was almost negligible in the SS/Diameter model, it was more evident in the SS/Height model (see Figure 2).

Table 2 presents the Pearson correlation coefficient between simulations and observations, and the various measured errors. In Figure 3 the standardized residuals of the simulations are plotted versus the observations, and the model predictors (tree size, light availability, and competition, even if the latter was not included in all models). There were only minor signs of heteroscedasticity in all models when the residuals were plotted versus the fitted values, indication that it was properly corrected by using the power variance in the model. Considering the residual distribution versus the model predictors, there were different patterns for each model: a slight overprediction only for the largest trees for SS/Height; slight underprediction for SS/Diameter and WH/Diameter at mid-light availability; and underprediction only towards the end-range of light for WH/Height and DF/Height. The resulting values of Mean Absolute Percentage Error (MAPE) were lowest for the western hemlock models (27% and 32% for height and DRC), then higher for the Sitka spruce models (38-39% for height and DRC), and highest for the Douglas fir height model (62%). It must be noted that the MAPE was influenced in all cases by few but very large relative errors for the trees showing the smallest growth.

Intra-regeneration competition was included in three models, affecting the growth rate for the SS/Height ( $K2 < 0$ ), and the asymptotic growth for the SS/Diameter and WH/Diameter models ( $A2 < 0$ ) (see Figure 4). The resulting effect in the first model (SS/Height) was to decrease the absolute growth especially at lower light levels, with a reduced impact as the light availability increases, while in the last two models (SS/Diameter and WH/Diameter) the reduction was the same in relative terms across all light levels.

The comparison of the species-specific absolute growth shows at low light a general advantage of WH over SS, and of SS over DF, that is then reversed at high light, with some exceptions. In Figure 5 (graphs a-d) we simulated growth values for medium-sized trees (height = 130 cm, DRC = 12 mm) in the absence of competition (a and b), or under strong competition, 25 trees per plot (c and d). For height growth, WH had the highest absolute values at almost all light levels for both scenarios. In the absence of competition, for the height growth, SS had higher values below GSF 0.2 than DF, while above it was the opposite; for the diameter growth, WH had higher absolute values than SS below GSF 0.4, and the opposite above. With strong levels of competition, at low light the advantage in height growth of SS over DF decreased markedly, and at high light the advantage in DRC of SS over WH totally disappeared. For trees of increasing sizes, SS had a slightly increasing advantage for growth at low light over DF (results not shown).

Figure 5 (graph e) shows how tree size affected the growth rate in the height models for all species, by plotting the light level necessary to reach the half-maximum-growth in the absence of competition. For SS/Height and WH/Height, this light level decreased with increasing tree size. For SS and WH, it decreased respectively from around GSF 0.25 and GSF 0.35 for a small tree (20 cm height), to GSF 0.18 and GSF 0.22 for a big tree (400 cm height). For DF/Height, it was GSF 0.29 for trees of all sizes. Again, the analysis for western hemlock, and partly for



DF, could have been biased due to the lack of sampled trees growing at high light levels. For SS/Diameter and WH/Diameter, the light necessary for half-maximum-growth was respectively GSF 0.37 and 0.17, in the absence of competition, for trees of all sizes. As reference, we estimated that the study sites received a daily photosynthetic photon flux density of around 53-56 moles per square meter (at the Earth surface), averaged during the vegetative period from mid-April to mid-September, with little variation from the southernmost to the northernmost site.

### 1.3.2 Crown plasticity analyses

Table 3 presents the best models describing ADR and LCR as a function of light. The final model for ADR included only light availability with a positive effect (Figure 6, graph a). There were no significant differences between SS and DF, so the same model was fitted to both species. The threshold of 20-25% of full light indicated in the literature for good growth of Sitka spruce would correspond to an ADR of 1.2-1.4 using such model. For the LCR model, light availability again had a positive effect (Figure 6, graph b), but that was mediated by species-specific differences (an interaction effect between light and species). WH had always the highest LCR values, with LCR being almost unaffected by light. SS had significantly higher LCR than DF, but the difference decreased towards higher light levels. Table 3 also presents the details for the species-specific models simulating height growth as a function of the previous year's apical dominance ratio (ADRp). We could calibrate a model for both DF and SS, however the fit was better for SS than DF (Figure 6, graph c and d). In both cases, the height growth significantly increased with both ADRp and tree height (Figure 6, graph d). The model shows that for SS trees with an ADRp around 1.2 (the value of the coefficient K) had growth the following year equal to half the maximum growth observed in the field.

## 1.4 Discussion

The growth models presented here can be used to support planning in CCF management, by simulating the potential growth response of natural regeneration to different levels of light under a canopy, and for further prospective analyses. The use of light availability as the main predictor makes these models well suited to describing the regeneration growth in those uneven-aged, mixed-species forest stands that could be the result of continuous cover forestry management in the UK. The simulated values of each model were biologically sound and fitted well the observations, although in all models there was a tendency to under-predict the growth of medium/large-sized trees growing at low/medium levels of light. We demonstrated that different non-linear structures are best suited to simulating different species-specific light-growth relationships. These relationships may also vary for the height and diameter growth in the same species.

For western hemlock, and to some extent also for Douglas fir, there was lack of data on trees growing at full light, which especially for the former may have affected the analysis. However, we covered the critical range of low-medium light levels most likely to be encountered in continuous cover forestry stands, and where the growth performance is more influenced by light and less by other environmental factors (Carter and Klinka, 1992). It was observed in other studies that the net photosynthesis in western hemlock and Douglas fir already reached saturation towards light levels of 30-40% full sunlight (Carter and Klinka, 1992; Grossnickle and Arnott, 1992; Leverenz and Jarvis, 1980). For the Sitka spruce height model only, the final structure based on the Logistic function showed an unlikely positive growth at zero light, even if it was very limited. We did not sample Sitka spruce trees growing at very low levels of light, but due to the sampling design followed we cannot conclusively state that there were none growing and surviving in those conditions. A more thorough sampling at those critical levels of light would be necessary to improve the model, which showed an unrealistic positive growth

at zero light. With the data available, the Logistic model showed the best fit under all statistical analysis. It must also be noted that hemispherical photography has been shown to be a poor predictor of light transmitted through dense canopies, i.e. at values of GSF 0.1 and less (Hale et al., 2009). Moreover, our study did not consider how light can vary throughout the years in continuous cover forestry, and consequently how the trees react to a changing light environment. For this reason, there may be the need to establish long-term field studies or controlled shading experiment. Climatic variables were not considered, since collecting micro-climatic information within the stands was not possible due to lack of time and resources. The climate below a canopy can vary from open conditions according to the tree density (Sellars, 2005). Finally, some of the Douglas fir trees were underplanted (although not recently) and may have had a different growth pattern.

The inclusion of tree size as an additional predictor always improved the fit. Tree size had a significant effect in increasing the maximum growth in all models, both for height and diameter. Larger trees as a consequence had a greater absolute growth at all light levels, due mostly to an increased capacity for light absorption and partly to an increased efficiency of light use (Binkley et al., 2013). We observed that for height growth in Sitka spruce and western hemlock, bigger trees compared to smaller trees had a slight additional advantage at low light, since they reached the half-maximum-growth at lower light levels (see Figure 5, graph e). It is possible that larger regenerating trees are able to use their accumulated reserves to survive short periods of reduction in light when compared to smaller ones (Delagrange et al., 2004), and this could contribute to their growth advantage over small trees at low light (and maybe also contributed to predict a positive growth at zero light, see before). Further work to analyse the interaction between light availability and size for the growth processes may be necessary.

Intra-regeneration competition significantly decreased the growth in the Sitka spruce height and diameter models, and in the western hemlock diameter model. The negative effect of

competition in the Sitka spruce height model decreased at higher light levels, consistent with the findings of Hasenauer & Kindermann (2006) and Collet & Chenost (2006), while in the diameter above root collar models for both Sitka spruce and western hemlock the growth was reduced similarly at all light levels. The results suggest that height growth of regenerating trees may be less affected by competition than diameter growth (Collet and Chenost, 2006; van Couwenberghe et al., 2013). Trees growing in dense patches but with almost full sunlight above them may have vertical growth that is not affected by competition while reducing their radial growth. We are aware of studies where only the radial and not the height growth of trees was affected by intra-regeneration competition (Collet and Chenost, 2006; van Couwenberghe et al., 2013), but not of the contrary. On the question of why some combinations of species and growth were affected by competition and others not, the results did not shed more light on the already mixed review presented in the introduction. Further work, such as improving the measure of competition by considering the size, distance and species of the competitors, is needed to clarify the effects of intra-regeneration competition.

For Douglas fir and Sitka spruce, both the apical dominance ratio and the live crown ratio increased with increasing light, with a pattern similar to that observed for other conifer species by Duchesneau et al. (2001) and Grassi & Giannini (2005). This confirmed the ability of these species to react to low light levels by changing their crown architecture. We did not observe differences between Sitka spruce and Douglas fir when modelling the apical dominance ratio as a function of light availability. However, there were significant differences in the live crown ratio: Douglas fir maintained a shorter crown than Sitka spruce especially at lower light levels. Conversely, western hemlock seemed almost unaffected by light availability and maintained a full live crown at all levels of light. Grassi & Giannini (2005) suggested that the apical dominance and live crown ratio patterns may shift as the trees gain in size, but this was not observed in this study, consistent with the results of Williams et al. (1999). We found intra-

regeneration competition significant neither for the apical dominance nor for the live crown ratio.

For both Douglas fir and Sitka spruce, we could fit models of height growth as a function of the apical dominance ratio of the previous year, even if for the former the results were not very accurate. For Sitka spruce, a value of apical dominance ratio of 1.2 corresponded to half of the maximum potential height growth in the next year. This result is slightly higher to those of Grassi & Giannini (2005) (for *Picea abies* and *Abies alba*) and Page *et al.* (2001) (for Sitka spruce), who considered trees with an apical dominance ratio equal to or less than 1 to be “in check”. The threshold of 20-25% of full light for good growth in Sitka spruce for the UK (Mason 2015) applied to the model of apical dominance ratio as a function of light gives an apical dominance ratio of 1.2-1.4. We thus suggest using as a quick assessment tool in the field an apical dominance ratio of 1.5 (more conservative and simpler to measure) for identifying Sitka spruce regenerating trees with an adequate growth potential.

Overall, observing all the parameters considered in this study, we define a shade tolerance ranking as Douglas fir  $\leq$  Sitka spruce  $<$  western hemlock, similar to the one identified by Mason *et al.* (2004). However, considering only one parameter could be misleading. Douglas fir compared to Sitka spruce had only slightly slower growth at low light but more evident faster growth at high light. Western hemlock had the greatest height growth at all light levels, maybe due to an intrinsic difference in the canopy architecture: a very thin, drooping, and elongated leader, with no clear lateral shoots. Kunstler *et al.* (2005) also showed that a more shade-tolerant species (*Fagus sylvatica* L.) had height growth higher at all light levels than a less shade-tolerant one (*Quercus pubescens* Willd.). When comparing the diameter growth, the higher shade-tolerance of western hemlock was evident: it had a faster radial growth than Sitka spruce at low light and the opposite at high light, as observed in their natural range (Minore, 1979; Taylor, 1990). Similar to Petritan *et al.*, (2009), more shade tolerant species (western

hemlock and then Sitka spruce) had in this study higher live crown ratio, indication as high tolerance to self-shading. The fact that under high intra-regeneration competition the Sitka spruce advantage at high light disappeared may be another indication of higher shade tolerance in western hemlock, which can better resist the lateral shading from other regenerating trees. For the three species, the best growth models belonged to different families, reflecting their different growth patterns. Only for Douglas fir was the Asymptotic-with-offset equation selected, indicative of lower shade tolerance than Sitka spruce and western hemlock (even if, as discussed already, some lack of sampling at very low light levels may have affected the analyses). The identification of a compensation point above zero light for Douglas fir suggests a lower capacity of this species to survive at low light when compared to both Sitka spruce and western hemlock. Better studies of survivorship of these species at low light must be however addressed to integrate the shade tolerance comparison carried out in this research.

We demonstrated that all the target species thrive relatively well at the light levels that can be commonly achieved in conifer stands managed with shelterwood systems, and that can be used as reference target by forest managers (GSF 0.20-0.30). Foresters aiming at mixed-species stands in the UK could obtain an adequate regeneration growth of all these species at the same time. For maintaining a viable presence of Douglas fir, however it seems likely that more constant thinning will have to be carried out to keep the light always at around that level (and at least above 10% of full light), while western hemlock, and to a lesser extent Sitka spruce, will be able to keep growing for some periods also at higher shading. It is likely that successional dynamics in a mixed-stand of species with such similar light requirements may be affected more crucially by variations in regeneration occurrence and survival (Wright et al., 1998), which could not be addressed in this study. The results show that is no need to release the regeneration early, since all the target species could achieve a growth very similar to the maximum at 50% of light. In addition, for the study species, this study did not show that trees

of bigger sizes require higher light availability and thus ever larger openings for their sustained growth. For Sitka spruce only, the quick indicator of apical dominance ratio of 1.5 can be used in the field to identify adequate growing conditions. For competition, the results showed that it affects more the diameter growth than the height growth. However, in case forest managers would be interested in higher diameter growth, the need to intervene with thinning of regenerating trees (i.e. respacing) could be assessed only after studies of mortality and self-thinning of the regeneration.

We conclude that modelling light-growth requires species-specific non-linear functions and that predictions are improved by including size and competition. The developed predictive models for height and diameter growth will allow accurate modelling of the study species in CCF management.

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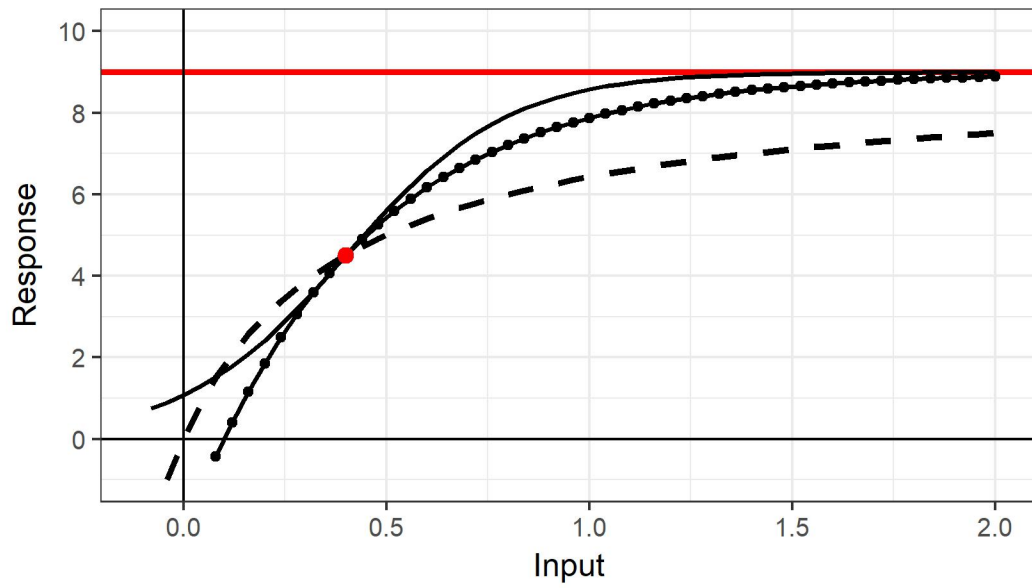


Figure 1. Examples of a Michaelis-Menten (dashed line), Logistic (continuous line) and Asymptotic-with-offset (dotted-continuous line) functions. All the functions were set to reach the same asymptotic response towards high values of input (represented by the red continuous line, response = 9). Note the Michaelis-Menten will reach it at higher values of input outside the graph. The growth rate parameter in all functions controls the value of input about which the response is half of the asymptote (represented by the red dot), and it was set equal for all of them (input = 0.4). Note also the different behaviour at zero input.

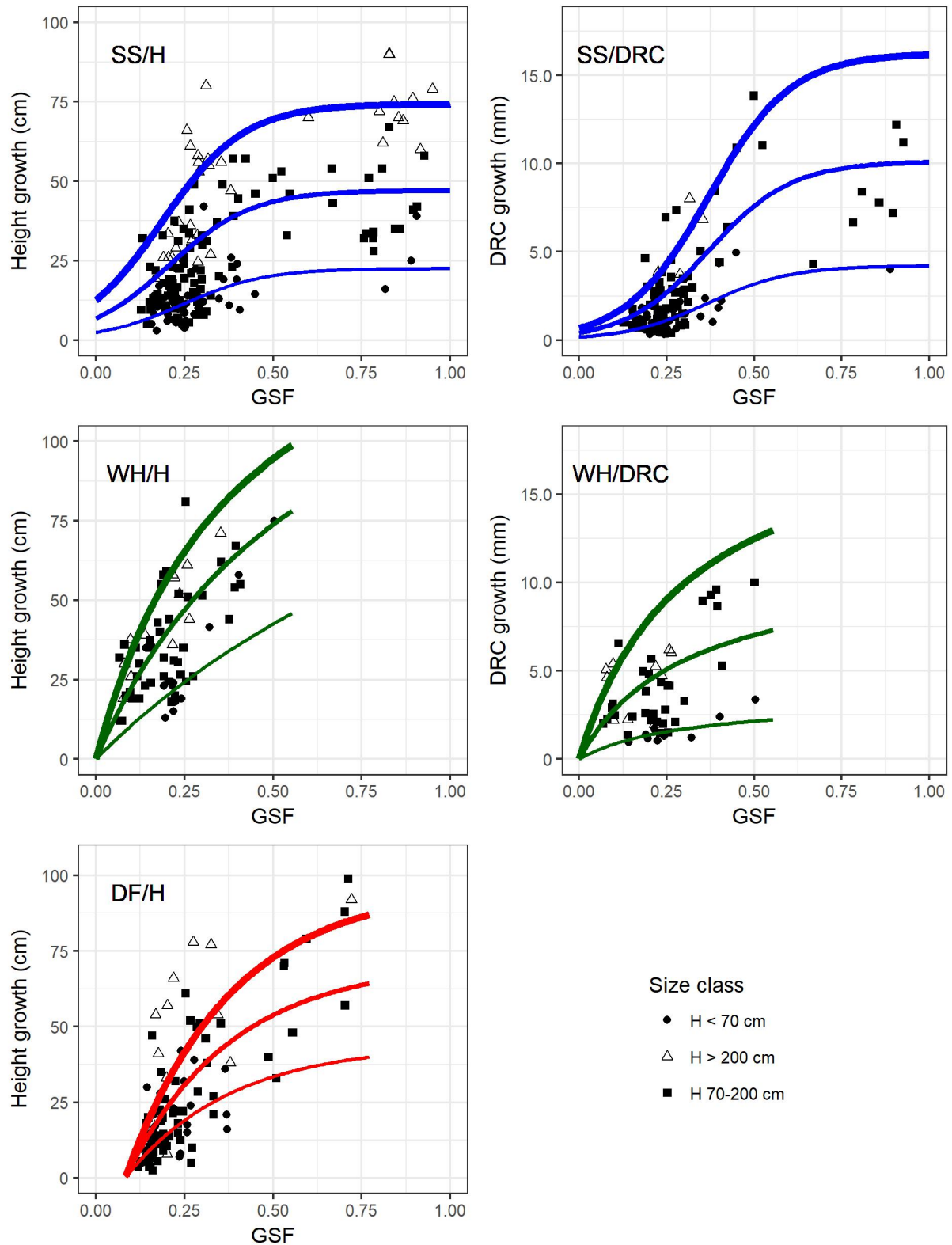


Figure 2. Simulated (lines) and observed (points) growth as function of light (GSF, Global Site Factor), for trees of different sizes, in absence of competition. SS, Sitka spruce; DF, Douglas fir; WH, western hemlock; H, Height; DRC, Diameter above Root Collar. In each graph: top line, simulated growth for a tree having size (height or diameter) equal to the 95% quantile of the population, medium line, to the mean, and bottom line, to the 5% quantile.



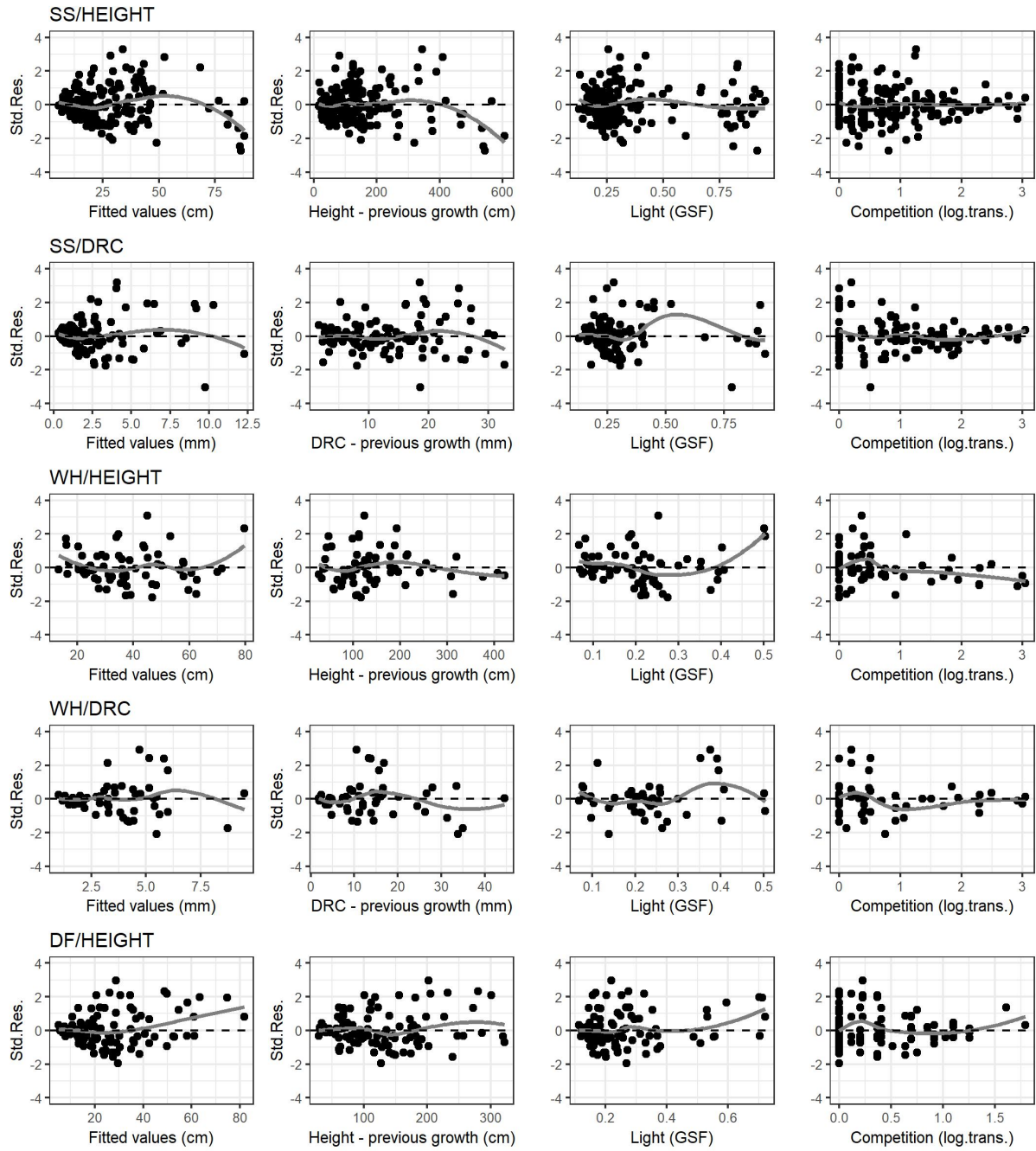


Figure 3. Standardized residuals plotted against the observed growth, the size previous the growth, the light availability (GSF, Global Site Factor) and the intra-regeneration competition (log-transformed plus 1). SS, Sitka spruce; DF, Douglas fir; WH, western hemlock; DRC, diameter above root collar. Continuous lines, LOESS (locally weighted scatterplot smoothing) curves.

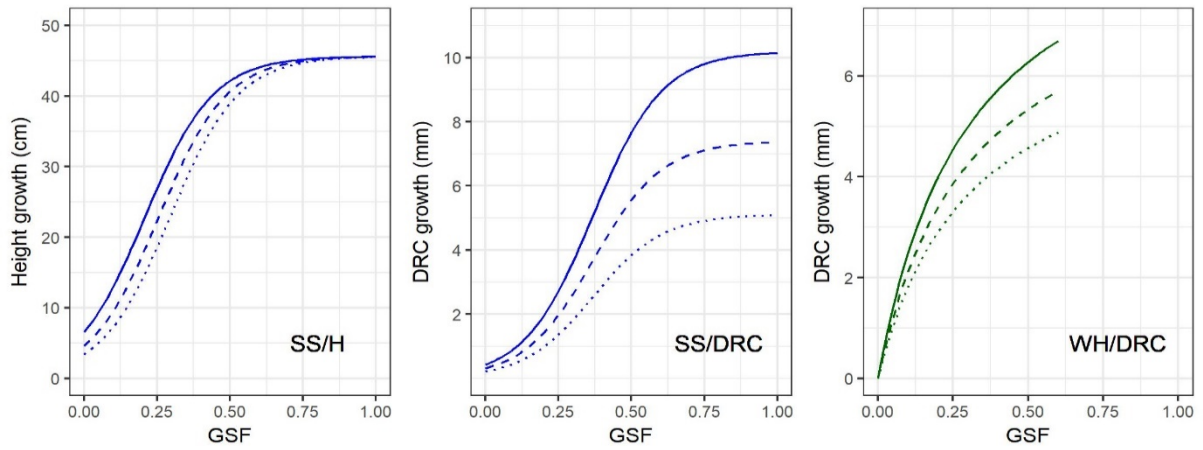


Figure 4. Simulated growth as function of light (GSF, Global Site Factor) under different competition levels. SS, Sitka spruce; WH, western hemlock; H, Height; DRC, Diameter above Root Collar. For height growth, a tree of height 130 cm was considered; for DRC growth, of DRC 12 mm. Continuous lines, no competition; dashed lines, low competition (5 trees/plot); dotted lines, high competition (25 trees/plot).

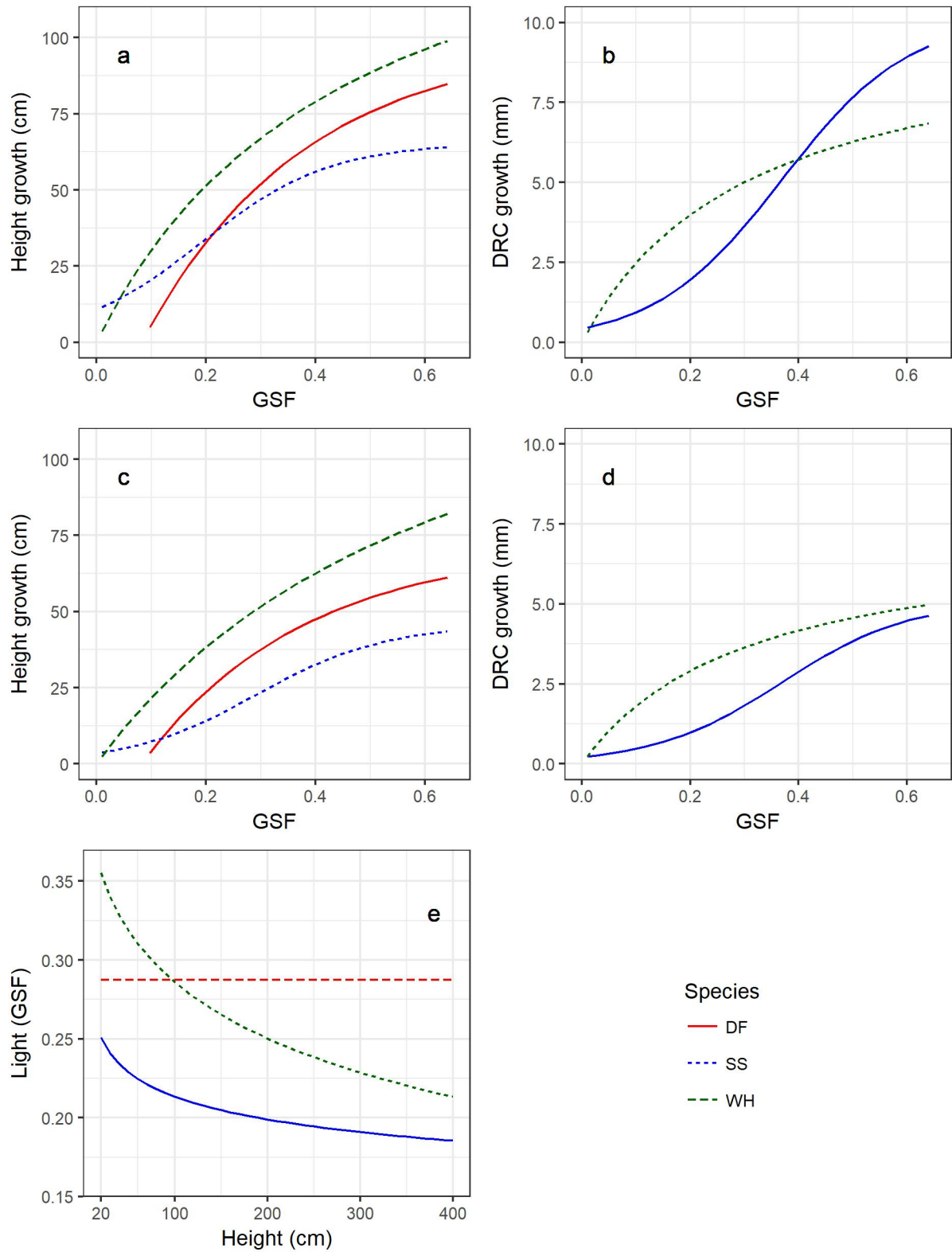


Figure 5. Graphs a-d. Comparison of species-specific simulated growth as function of light (GSF, Global Site Factor), in absence of competition (a and b) and under strong competition (25 trees/plot, c and d). DF, Douglas fir; SS, Sitka spruce; WH, western hemlock. The height growth was simulated for trees of 130 cm height; the diameter above root collar (DRC) growth for trees of DRC 12 mm. Graph e: light level necessary for height growth equal to half the maximum growth at full light, as function of tree size.

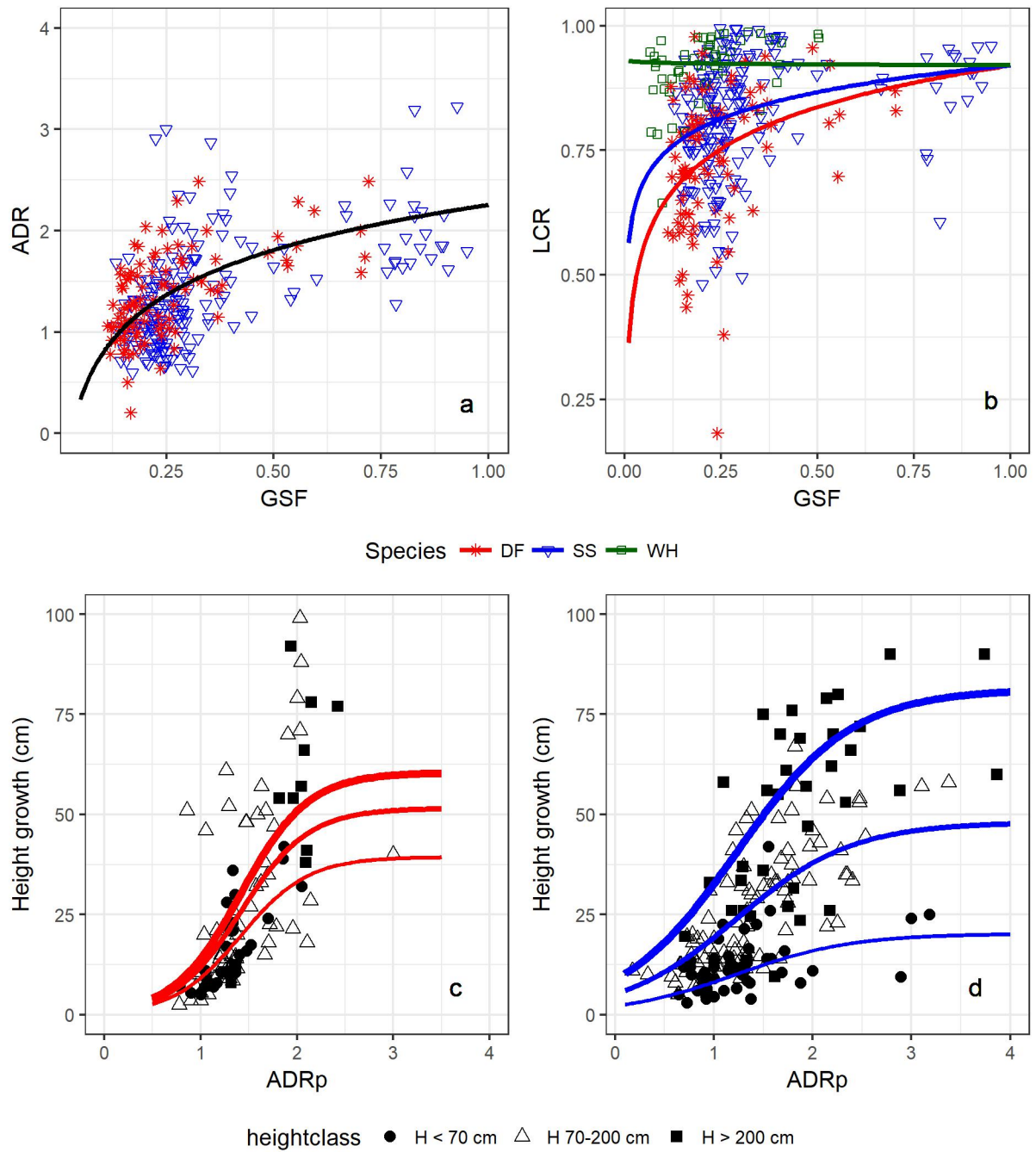


Figure 6. Simulated (lines) and observed (points) for: graph a, Apical Dominance Ratio (ADR) as function of light availability (GSF, Global Site Factor), the continuous black line is for both Douglas fir (DF) and Sitka spruce (SS); graph b: Live Crown Ratio (LCR) as function of light availability (GSF, Global Site Factor) and species (WH, western hemlock); graphs c and d, respectively Douglas fir and Sitka spruce height growth as function of Apical Dominance Ratio of the previous year (ADRp) and tree size: from top to bottom in both graphs, the lines are for trees respectively having height equal to the 95% quantile of the population considered, to the mean, and to the 5% quantile.

Table 1. Details of study areas and tree measured. Values of light (GSF, Global Site Facto) and size are given as minimum-mean-maximum. Height, height before the last growth season, DRC, diameter at 10 cm above root collar; n, the sample size. Larch, *Larix spp.*; Spruce, *Picea abies* and *Picea sitchensis*, Douglas fir, *Pseudotsuga menziesii*, Scots pine, *Pinus sylvestris*; mixed broadleaves, *Acer spp.*, *Fagus sylvatica* and *Quercus spp.*

Forest	Coordinates (WGS84)	Canopy species	Light (GSF)	Sitka spruce				Western hemlock				Douglas fir	
				Height (cm)	n	DRC (mm)	n	Height (cm)	n	DRC (mm)	n	Height (cm)	n
Aberfoyle (Scotland)	56° 13' N 4° 21' W	Larch, spruce	0.13-0.25-0.39	25-151-410	31	2-14-25	19	-	-		-	-	-
Clocaenog (Wales)	53° 04' N 3° 24' W	Spruce, Larch	0.12-0.41-0.95	21-184-607	89	1-12-30	34	27-108-407	20	2-9-27	18	61-116-230	18
Coed-Y- Brenin (Wales)	52° 48' N 3° 53' W	Douglas fir, mixed broadleaves	0.13-0.18-0.25	-	-	-	-	112-137-188	4	17-21-26	4	31-137-322	18
Gwydyr (Wales)	53° 05' N 3° 48' W	Douglas fir, mixed broadleaves, Scots pine	0.07-0.18-0.38	45-124-200	16	-	-	83-138-190	10	-	-	41-76-133	11
Kielder (England)	55° 13' N 2° 27' W	Spruce	0.16-0.24-0.38	15-87-241	49	3-10-27	33	75-175-271	6	5-13-24	6	-	-
Lakes district (England)	54° 30' N 3° 09' W	Douglas fir	0.12-0.24-0.83	34-133-243	18	3-15-31	5	79-175-271	5	12-14-16	3	29-130-301	25
Mortimer (England)	52° 21' N 2° 45' W	Mixed broadleaves, Douglas fir	0.07-0.15-0.34	-	-	-	-	91-191-376	10	11-23-45	9	34-170-286	13
Wykeham (England)	54° 16' N 0° 33' W	Larch, Scots pine, spruce	0.11-0.28-0.53	16-113-320	30	2-12-33	26	33-157-422	11	2-13-35	11	41-113-272	16
<b>Total</b>			<b>0.07-0.40-0.95</b>	<b>15-140-607</b>	<b>187</b>	<b>2-12-33</b>	<b>117</b>	<b>27-145-422</b>	<b>66</b>	<b>2-12-45</b>	<b>51</b>	<b>29-125-322</b>	<b>101</b>

Table 2. Best growth model for each case, showing the family of the equation. SS, Sitka spruce; DF, Douglas fir; WH, western hemlock; H, height; DRC, diameter above root collar. Empty cell: the coefficient was excluded in the best model. NA: the coefficient does not appear in the equation used. Then, *r* is the Pearson correlations coefficient between simulations and observations; RMSE, the Root-Mean-Square-Error (in cm for height and mm for diameter); MAE, the Mean Absolute Error (in cm for height and mm for diameter); MAPE, the MAE relative to the observations.

Model	Coefficient													
	A	K	A2	K2	C	S	Pa	Pk	Ps	Pc	r	RMSE	MAE	MAPE
<b>SS/HEIGHT (n=187) - Logistic</b>														
Value	5.624	0.340	-	-0.043	NA	0.117	0.430	0.101	-	NA	0.88	9.5	7.1	37.6%
p-value	0.003	0.003	-	0.014	NA	0.000	0.000	0.106	-	NA				
<b>SS/DRC (n=117) - Logistic</b>														
Value	2.406	0.369	-0.369	-	NA	0.118	0.581	-	-	NA	0.94	0.9	0.6	39.0%
p-value	<0.001	<0.001	<0.001	-	NA	<0.001	<0.001	-	-	NA				
<b>WH/HEIGHT (n=66) - Michaelis-Menten</b>														
Value	170.9	7.033	-	-	NA	NA	-	0.476	NA	NA	0.79	11.6	8.8	27.0%
p-value	0.005	0.048	-	-	NA	NA	-	<0.001	NA	NA				
<b>WH/DRC (n=51) - Michaelis-Menten</b>														
Value	1.936	0.308	-0.161	-	NA	NA	0.666	-	NA	NA	0.76	1.5	1.1	32.5%
p-value	0.003	0.055	0.070	-	NA	NA	<0.001	-	NA	NA				
<b>DF/HEIGHT (n=101) - Asymptotic-with-offset</b>														
Value	10.809	1.219	-	-	0.083	NA	0.390	-	NA	-	0.84	12.5	9.6	61.6%
p-value	0.061	0.010	-	-	<0.001	NA	<0.001	-	NA	-				

Table 3. Details for the models describing (a) apical dominance ratio (ADR) as function of light (GSF, Global Site Factor); (b) Live Crown Ratio (LCR) as function of light and species; (c) and (d), the height growth respectively of Douglas fir and Sitka spruce as function of ADR of the previous year (ADRp). It is indicated whether the model is based on a Generalized Linear Mixed Model (GLMM) or on the non-linear Logistic equation. Hp, is the height of the tree in the previous year, SS is Sitka spruce, WH is western hemlock.

<b>(a) ADR = f(light) (n=284) - GLMM</b>				
<b>Coefficient</b>	<b>Intercept</b>	<b>log(GSF)</b>		
<b>Value</b>	2.254	0.641		
<b>p-value</b>	<0.001	<0.001		
<b>(b) LCR = f(light) (n=331) - GLMM</b>				
<b>Coefficient</b>	<b>Intercept</b>	<b>log(GSF)</b>	<b>log(GSF):SS</b>	<b>log(GSF):WH</b>
<b>Value</b>	0.921	0.121	-0.043	-0.123
<b>p-value</b>	<0.001	<0.001	<0.001	<0.001
<b>(c) DF/Height = f(ADRp) (n=98) - Logistic</b>				
<b>Coefficient</b>	<b>A</b>	<b>K</b>	<b>S</b>	<b>Pa</b>
<b>Value</b>	18.202	1.416	0.349	0.217
<b>p-value</b>	0.102	<0.001	<0.001	0.035
<b>(d) SS/Height = f(ADRp) (n=180) - Logistic</b>				
<b>Coefficient</b>	<b>A</b>	<b>K</b>	<b>S</b>	<b>Pa</b>
<b>Value</b>	4.033	1.232	0.582	0.501
<b>p-value</b>	<0.001	<0.001	<0.001	<0.001

## SUPPLEMENTARY INFORMATION

We show here: Equation S 1, how to obtain the input value for half-maximum-growth in case of the Asymptotic-with-offset equation from the parameter  $lcr$ , considering the compensation point C; Table S.1, the summary of the biological effects of the various coefficients for the non-linear functions; Table S.2, the full list of Akaike Information Criteria (AIC) values for each model tested; Figure S.1, the schematics of the tree measurements; Figure S.2, the 95% prediction intervals for each model. For the latter, the 95% prediction intervals for each model were calculated for each model by i) resampling 1,000 times the coefficients according to a multivariate distribution using the same variance-covariance of the calibrated model (using the package *MASS* from R Statistical Software); ii) calculating the predictions using all the new combinations of coefficients; iii) identify the 97.5% and 2.5% quantiles of those predicted values as upper and lower boundaries.

$$\text{Equation S 1: } Input = \log(2) / \exp(lcr) + C$$

Table S.1. Summary of the biological effects of the various coefficients used in the non-linear functions

<b>Asym</b>	<b>All equations</b>	<b>A</b>	Value of maximum growth (in cm or mm).
		<b>A2</b>	Effect of competition on the maximum growth: if 0, it is null; if negative, it decreases the maximum growth.
		<b>Pa</b>	Effect of tree size on the maximum growth: null at 0, then increases the maximum growth with a stronger effect as this parameter increases.
<b>xmid/lcr</b>	<b>All equations</b>	<b>K</b>	Correlated to the growth rate to reach the maximum growth: for <i>xmid</i> , the higher the value, the slower the rate; for <i>lcr</i> , the opposite. Also, different scale for the different equations.
		<b>K2</b>	Effect of competition on the growth rate: if 0, it is null; if negative, it decreases the growth rate, both in <i>xmid</i> and <i>rate</i> .
		<b>Pk</b>	Effect of tree size on the growth rate: null at 0, then increases the growth rate with a stronger effect as this parameter increases, both in <i>xmid</i> and <i>lcr</i> .
<b>scale</b>	<b>Logistic</b>	<b>S</b>	Positively correlated to the steepness of the sigmoid curve.
		<b>Ps</b>	Effect of tree size on the steepness of the sigmoid curve: null at 0, then increases the steepness with a stronger effect as this parameter increases.
<b>cp</b>	<b>Asymptotic-with-offset</b>	<b>C</b>	Light level (GSF) equivalent to null growth (compensation point).
		<b>Pc</b>	Effect of tree size on the compensation point: null at 0, then decreases the compensation point with a stronger effect going towards 1 and above.

Table S.2. Akaike Information Criteria (AIC) for all models from each equation and combination species/growth. *SS* is Sitka spruce, *DF* is Douglas fir, *WH* is western hemlock, *H* is Height, *DRC* is diameter above root collar. Under Size and



Competition, it is indicated which main parameters of the equation were influenced by respectively tree size and intra-regeneration competition. An empty cell means that a model could not be successfully calibrated. For each combination species/growth: bold, all the models considered in the group of best candidates (difference in AIC less than 2 points from the model with lowest AIC, models with no biological validity discarded); bold, italicized and in red, the best model selected for each combination growth/species

Equation	Size	Competition	SS/H	SS/DRC	WH/H	WH/DRC	DF/H
Logistic	None	None	1509	-	-	-	830
Logistic	None	A	1512	-	-	-	831
Logistic	None	K	-	-	-	-	-
Logistic	A	None	1357	315	-	173	794
Logistic	A	A	1345	<b>283</b>	-	<b>171</b>	795
Logistic	A	K	1345	<b>284</b>	-	<b>171</b>	796
Logistic	K	None	1406	333	-	-	813
Logistic	K	A	1398	304	-	-	808
Logistic	K	K	1386	305	-	-	809
Logistic	S	None	1401	-	-	-	821
Logistic	S	A	1393	339	-	-	-
Logistic	S	K	1392	339	-	-	-
Logistic	A-K	None	1354	315	-	-	795
Logistic	A-K	A	1345	<b>284</b>	-	173	796
Logistic	A-K	K	<b>1340</b>	286	517	<b>170</b>	806
Logistic	A-S	None	1357	347	-	176	794
Logistic	A-S	A	-	285	-	173	795
Logistic	A-S	K	1347	-	-	-	796
Logistic	K-S	None	1359	315	-	-	798
Logistic	K-S	A	-	292	-	<b>172</b>	-
Logistic	K-S	K	-	295	-	173	-
Logistic	A-K-S	None	1349	313	-	-	795
Logistic	A-K-S	A	1344	286	-	169	796
Logistic	A-K-S	K	<b>1339</b>	289	-	174	797
Michaelis-Menten	None	None	1516	-	541	233	-
Michaelis-Menten	None	A	1518	-	-	-	-
Michaelis-Menten	None	K	1517	628	-	225	-
Michaelis-Menten	A	None	1370	-	521	178	-
Michaelis-Menten	A	A	1359	-	607	<b>171</b>	-
Michaelis-Menten	A	K	1358	-	-	<b>172</b>	-
Michaelis-Menten	K	None	1365	617	<b>519</b>	177	1014
Michaelis-Menten	K	A	1359	629	<b>518</b>	-	1011
Michaelis-Menten	K	K	1356	652	-	173	-
Michaelis-Menten	A-K	None	1366	-	-	179	-
Michaelis-Menten	A-K	A	-	-	-	-	-
Michaelis-Menten	A-K	K	-	-	-	-	-
Asymptotic-with-offset	None	None	-	-	-	-	-
Asymptotic-with-offset	None	A	-	-	-	-	-
Asymptotic-with-offset	None	K	-	-	-	-	-

Asymptotic-with-offset	A	None	1365	-	-	-	790
Asymptotic-with-offset	A	A	1353	313	-	-	801
Asymptotic-with-offset	A	K	1353	-	-	-	-
Asymptotic-with-offset	K	None	1377	-	-	-	793
Asymptotic-with-offset	K	A	1371	-	524	-	795
Asymptotic-with-offset	K	K	-	335	-	-	-
Asymptotic-with-offset	C	None	-	-	-	-	-
Asymptotic-with-offset	C	A	-	-	-	-	-
Asymptotic-with-offset	C	K	-	-	-	-	-
Asymptotic-with-offset	A-K	None	1353	-	-	-	-
Asymptotic-with-offset	A-K	A	-	-	-	-	801
Asymptotic-with-offset	A-K	K	1347	-	-	-	-
Asymptotic-with-offset	A-C	None	1365	-	-	-	800
Asymptotic-with-offset	A-C	A	1355	-	-	-	802
Asymptotic-with-offset	A-C	K	1353	-	-	-	-
Asymptotic-with-offset	K-C	None	1368	369	-	-	-
Asymptotic-with-offset	K-C	A	-	-	-	-	-
Asymptotic-with-offset	K-C	K	-	-	-	-	-
Asymptotic-with-offset	A-K-C	None	1354	-	-	-	-
Asymptotic-with-offset	A-K-C	A	-	-	-	-	-
Asymptotic-with-offset	A-K-C	K	-	-	-	-	-

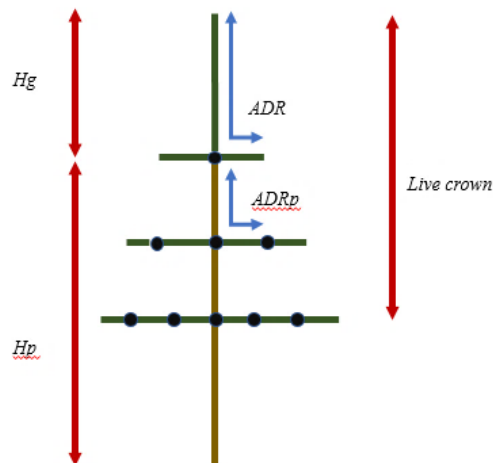


Figure S.1. Schematics of tree height and crown measurements. *Hg*, height growth; *Hp*, tree height before the growth; *ADR* and *ADRp*, the apical dominance ratio respectively of the current vegetative season and of the previous one (the arrows showing the corresponding leader and lateral shoots).

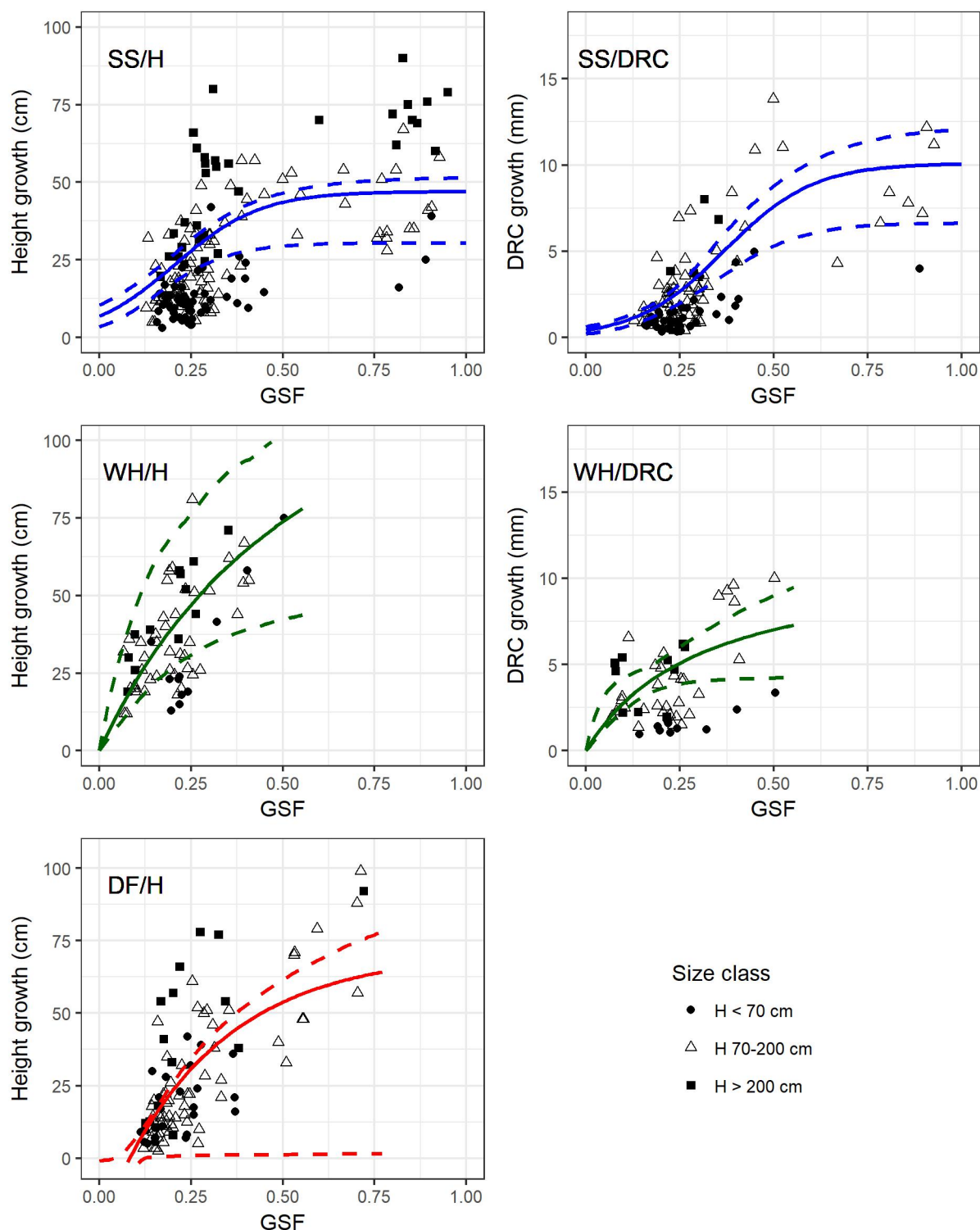


Figure S.2. Simulated growth patterns (continuous line) of each growth model as function of light (GSF, Global Site Factor), for a tree of average height or diameter, and in absence of competition, plotted with the observations (points). SS is Sitka spruce; DF, Douglas fir; WH, western hemlock; H, Height; DRC, Diameter above Root Collar; DBH, Diameter at Breast Height. The dashed lines are the upper and lower boundaries defining a 95% prediction Interval.